

Boston University College of Liberal Arts Library

THE GIFT OF The Author

AM.1930

an

June 1930

BOSTON UNIVERSITY GRADUATE SCHOOL

Thesis

EXPERIMENTS IN GENETICS AND EVOLUTION
ON THE PIGEON

Submitted by

James Grant Anderson

(A. B., Brown, 1914)

In partial fulfilment of requirements for the degree of Master of Arts

1930

p 6 3 6 5

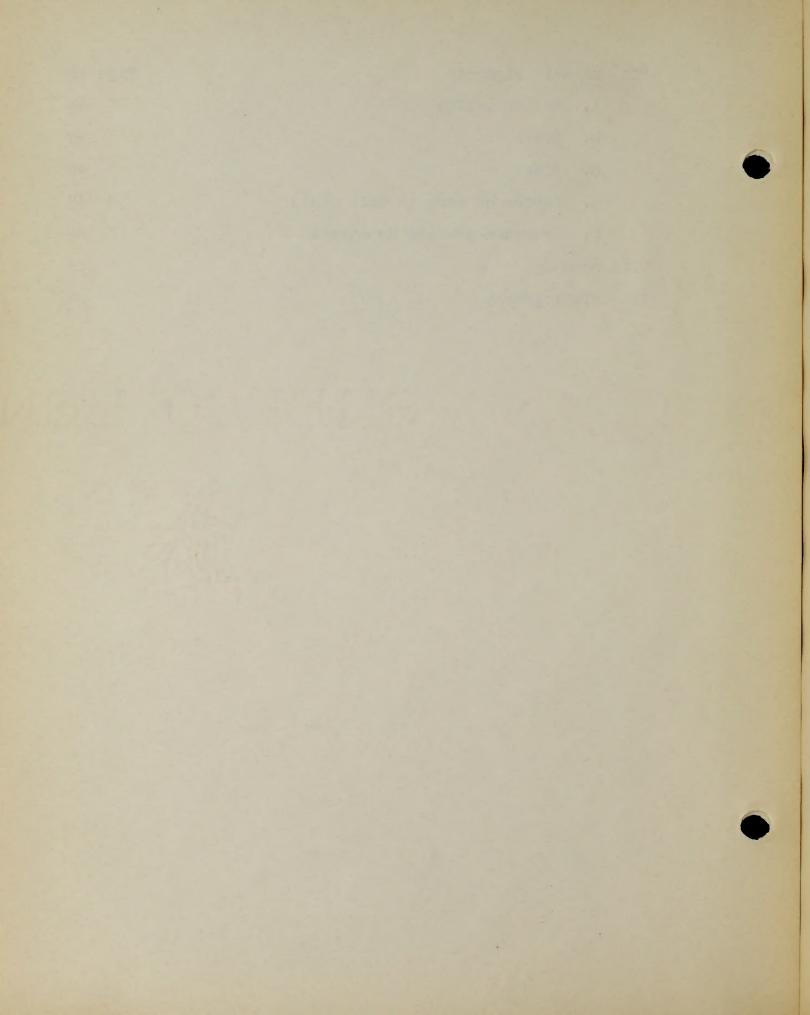
378.744 BO A.M. 1930 an

OUTLINE

c.1

THE	USE OF THE PIGEON IN EXPERIMENTAL GENETICS	AND EVOLUTION				
I	Introduction	Page 1				
	(1) Darwin's table	" 2				
II	Treatment of Darwin's work					
	1. Points in which all breeds agree	11 3				
	2. Selection	" 5				
	3. Common ancestry	11 7				
	4. Historical treatment	" 11				
	5. Darwin's breeding experiments	" 14				
III	Color pattern					
	1. Work of Charles Otis Whitman	" 16				
IV	Determination of sex	11 23				
	1. Whitman's conclusions	" 24				
	2. Reason for them advanced by Riddle	" 25				
	3. Cole's work on sex ratio	" 26				
	4. Crew's work	11 28				
V	Lace or silky	" 29				
VI	Color inheritance and breeding	" 34				
	1. Blue and black	" 36				
	2. Red	" 37				
	3. Lacing	" 37				
	4. White	11 39				
	5. Sex linked colors	" 39				

VII	Melanin pigments			42
	1.	Red or yellow	11	43
	2.	Black	11	44
	3.	Blue	11	45
	4.	Review of work in this field	11	47
	5.	Presence-absence hypothesis	tt	50
VIII	Summary		11	53
IX	Bibliography			58



THE USE OF THE PIGEON IN EXPERIMENTAL GENETICS AND EVOLUTION

Since there are over one hundred and fifty varieties of the domesticated pigeon, Columba livia, it would seem that any attempt at scientific study of its genetics or evolution must end in a mass of conflicting data. The very fact, however, that there are so many varieties offers just so much more chance to discover steps by which the advance has been made. Pigeon culture dates back into dim obscurity and it is an historical fact that they were highly prized by the ancient Romans. Pliny wrote of the interest displayed in breeding rare varieties. Eastern potentates have maintained aviaries containing thousands of rare specimens. Englishmen have expended their famous skill as live stock breeders in perfecting the various breeds and today there are literally thousands of Americans who find happiness in breeding pigeons. Their interest, however, is in the "fancy" side and scarcely any attempt has been made to develop the breeds along scientific lines. The first real impetus to scientific study of the pigeon race was given by Charles Darwin (1868). He used Columba livia to show that evolution had actually taken place.

The method used in this paper will be to deal first with Darwin's work, and then deal with the work of later investigators. Darwin, who was the pioneer in this field lacked many of the tools and controls of the modern investi-

or the descriptions of plants, this work to the to

to real to real and the land top of the plant of the land of the l

on	
Lge	
Pige	
Rock	
OF	
livia	
11.	
lumba	
Colu	

Group IV		\$wallow!	rugher ' ' ' ' ' 'English ' ' ' ' Frillback '
Group III	Tumbler	Tur	Fantail' 'Indian '''Laugher African 'Frillback' 'Eng Owl' 'Jacobin Frill' ' 'Jacobin Frill' ' 'Bhort ' '''
Sub' Group 2 3 4 5	-Murassa -Bussorah 11 Bagadotten	Dragoon	English Runt ' Barb Far
Group I Su	German Pouter	Dutch Pouter Lille P	English E Pouter C

gators, yet he performed interesting breeding tests and described many differences in structure and color. He tabulated the breeds of domesticated pigeons in a table which is here appended.

In this classification Darwin has merely skimmed the surface. In group one he has listed the so called "blowers", birds chiefly characterized by the ability to inflate the crop. In group two are the breeds which have peculiar structural properties such as excessively stout beaks, unduly developed wattles and eye ceres and exceptional size. In group three are the breeds characterized by peculiar feather growth. In this group he classed also the short faced pigeons, i.e., those in which the length of beak has been reduced to the minimum. In group four are the breeds chiefly remarkable for color and its distribution over the feathers. The trumpeter might well have been in group three for, in addition to its peculiar voice, it has remarkable feather formation.

There are several characteristics in which all breeds agree, for example, the number of tail feathers and the number of primary flight feathers is constant in all breeds and in most varieties. There are usually twelve tail feathers, but oriental rollers have more and fantails have been known to have as many as forty-two. Generally there are ten primaries, but Darwin had seen eight short-faced tumblers which had only nine and some other tumblers which had eleven primaries. The number of scutellae varies on the feet of pigeons of the same breed and also on the two feet of the same bird.

Another interesting fact noticed by Darwin and one which is only too well known to fancy pigeon breeders, is that the especial characters for which each breed is valued are variable. Thus in carriers the length and width of the skull, the curvature of the beak and the size and texture of the wattle vary greatly. In short faced tumblers the shortness of the beak, the prominence of the forehead and the carriage vary. Wherever there is a peculiar characteristic in one breed, the males will show this more pronouncedly than will the females. This fact in domesticated pigeons is in direct contrast to Columba livia in which there is no apparent difference between the male and female.

Darwin studied the skeletons of various breeds and discovered certain osteological differences. For example, the whole skull in its proportions, outlines and relative direction of the bones varies much in the different breeds. Thus, the carrier has elongated bones in the face and the space between the orbits is narrow. In the bagadotten the upper mandible is remarkably arched and the premaxillary bones are broader than those of the carrier. In the short-faced tumbler the skull is globular, the bones of the face are very short while the front of the skull and the descending nasal bones are almost perpendicular, the maxillojugal arch and premaxillary bones form almost a straight line. The space between the prominent edges of the orbits is depressed. In the barb the premaxillary bones are very short and their anterior part as well as the lower part of the nasal bone.

all in the contract of the con

is much thicker than in the rock pigeon. The degree of downward curvature in the distal half of the lower mandible varies greatly in the various breeds. It also varies greatly in individuals of the same breed. Breeders of dragoons have succeeded in producing specimens in which this downward curvature is completely absent. In some runts the symphysis of the lower jaw is solid. It is difficult to believe that skulls differing as much as above described could belong to the same species.

Darwin noticed that, in the Bussorah carrier, the twelfth cervical vertebrae carries a small rib. All breeds have eight dorsal vertebrae but there are variations as to size and shape. In Columba livia all eight bear ribs but the eighth rib is very thin and the seventh rib has no process. In pouters all the ribs are very broad and the seventh pair have distinct processes. Darwin examined some specimens of tumblers, nuns and fantails which had only seven ribs. There is considerable variation in the number of sacral vertebrae. Columba livia has twelve, the pouter has thirteen and other breeds are known to have eleven and twelve. The rock pigeon has seven caudal vertebrae while fantails have eight or nine and the shape varies.

Fanciers by careful selection have consciously increased one part and unconsciously increased others. Thus, one of the problems of the dragoon breeder has been to increase the size of the wattle upon the beak and simultaneously to decrease the size of the eye cere. In pouters elongation of the body is a selected character and the ribs have become

the state of the s

very broad, the seventh pair being furnished with processes, the sacral and caudal vertebrae have increased in number while the sternum has increased in length. In fantails the length and the number of caudal vertebrae has increased. Wings and tail feathers tend to vary in length together. This correlation is not intentional on the part of the fancier, for since 1600 jacobin fanciers have been trying to increase the length of feather in the hood and, accomplishing this, have brought about a corresponding increase in the length of the tail and wings. Hence, during this gradual process of selection and variation the external and internal structure of the various breeds have been modified in a correlated manner. Another case of correlation which was observed by Darwin was that when the feet are feathered, the roots of the feathers are connected by a web of skin and, in correlation, the two outer toes are connected by skin. Moreover, he noticed that there is a correlation between the length of the beak and the length of the feet. In short beaked birds the middle toe has decreased in length while in long beaked birds the length of the middle toe has increased.

The more highly prized pigeons are confined in aviaries and consequently, it may be said that all domestic pigeons are fed without going far afield in search of food. Hence, it ought to follow that those organs connected with flight have decreased in size. Darwin by careful measurements found this to be true. In domesticated pigeons the sternum was, on the average, one-third inch shorter than in the rock pigeon. A similar decrease was found in the furculum as well as in the scapula.

Common ancestry of pigeons

One of Darwin's most interesting conclusions was that all our breeds of domesticated pigeons came from a common ancestor. He said pigeons are social, i.e., they tend to live in flocks and they are not arboreal. Of the wild species of pigeons, which are naturally social and build their nests among the rocks, he listed Columba leuconata, which derives its name from the white bar across the tail. This species inhabits the heights of the Himalayas, so probably is not an ancestor of our domestic pigeons which thrive and breed in the tropics.

Darwin next listed Columba guinea which, he said, has notched feathers in the neck which no domestic pigeon shows. Columba oenas which will mate with Columba livia but the first filial generation of hybrids are sterile. This sterility of the first filial generation never occurs in the domestic pigeons so Columba guinea is eliminated.

Columba affinis of England is checquered and received little consideration from Darwin. Whitman (1919), on the other hand, did treat it fully. Columba intermedia of India resembles closely the blue rock pigeon except that it has a blue rump. Darwin said that when this breed is domesticated the checker pattern appears just as it does in the Columba livia. Here Darwin diverged strongly from Whitman and other present day geneticists who maintain that the production of the checker from the blue bar pattern is impossible.

The only wild pigeon which has a range equal to that of the domestic pigeon is Columba livia (including affinis, inter-

with the second second

media, etc.,) which has a range from the southern coast of Norway and the Faroe Islands to the Mediterranean, Madiera, the Canary Islands, Abyssinia, India, and Japan.

If the eleven principal races of domestic pigeons have not arisen from one race they must have had many ancestors for it would be impossible to produce so many variations by crossing only a few aboriginal breeds. The known history of many of the present day breeds dates back at least to 1600 and it is improbable that seven or eight distinct species could have been obliterated in that time. Wild birds are not likely to breed in captivity. So true is this that hardly one such breed has been reclaimed in the past three hundred years.

Pigeons do not become feral. This indicates that because they have undergone a long period of domestication they are unfitted for wild life. Moreover, if man has created the modern pigeon from seven or eight species he must have chosen highly abnormal species for no such abnormalities occur in wild species today. So we must suppose that all of their highly abnormal ancestors have become extinct.

Darwin listed the particulars in which all domestic races agree as follows. All domestic races of pigeons will pair and their offspring are fully fertile. All lay two eggs and this is not a universal rule with Columbidae. All have approximately the same incubation period, endure the same extremes of climate, prefer the same food, are fond of salt, exhibit same gestures when courting and all, except the trumpeters and laughers, coo in the same manner, which differs from the coo of any wild pigeon. The range of color of all

the state of the section of the section of

domestic pigeons is similar, they all have the metallic lustre on the neck and in addition all exhibit the peculiar correlation between the down and the adult plumage, which will be dealt with more fully later.

In breeds such as the fantails, pouters, carriers, jacobins etc., which show extreme variation in some parts, the
other parts remain nearly constant. It would be extremely
difficult to select six or eight parent species which would
exhibit this uniformity and, at the same time, have such
sharply contrasted abnormalities. Darwin explained this by
his theory of natural selection. He said changes in natural
species are preserved through utility and such changes lead
to changes in ways of life which in turn lead to other structural changes, whereas, if these structural changes have all
come about since domestication, there would be no change in
the way of life.

Darwin's most clinching argument was that Columba livia is slatey blue with two black bars on the wings, a black bar on the distal part of the tail, a white rump and the outer web of the outer tail feathers is white except near the end. This color pattern is unique with Columba livia and is particularly interesting in view of one of Darwin's famous breedind experiments. He crossed a mongrel female barb-fantail with a mongrel male barb-spot. Neither of these mongrels showed the slightest trace of blue, and blue barbs are very rare, yet the first filial progeny all came in the regulation blue barred pattern except for a red tint on the head and some of the same tint on the stomach. He considered this a case of reversion to the original color pattern. He also listed

and the same and the same and the same and

an instance of two blue barred tumblers producing a blue checkered offspring. There he was in sharp contrast with the modern theory that the checker pattern is the original pattern and that it is impossible to produce a checker pattern from two blue barred parents. In this connection a paper written by Mr. T. A. Havermeyer* is of interest. He crossed white fantails with blacks, blues, reds, and yellows to improve the type of the latter colors, and the first filial generation invariably produced the checker pattern. Thus, white bred to black produced blue checkers, while white bred to red or yellow produced dun checkers.

Whoever denies that all breeds have a common parentage must choose between three assumptions. First, that formerly there existed eight or nine species which, although aboriginally of varied color patterns, have yet varied in so exactly the same manner that they have come to possess the ordinary color pattern of Columba livia. This assumption fails to account for the continued occurence of the blue or checker patterns when crossing takes place. Second, that all eight or nine were colored like Columbe livia. This assumption is absurd for none of the Columbidae are so colored today. Third, that all races of domestic pigeons which have been bred with such care by fanciers have been crossed, within say twenty generations, with Columba livia and have thus acquired the tendency, when crossed, to revert to blue barred pigeons with white rumps etc. This is limited to twenty generations for, when only one cross has been made, each succeeding generation reduces the tendency to

^{*} Pigeon News, Boston August 1929

reversion as each carries less and less of the blood of its ancestor. When there has been no cross with a distinct breed and yet there is a tendency in both parents to revert to some long lost ancestor, this tendency is apparently transmitted undiminished for untold generations. Thus there are two distinct types of reversion which are irreconcilable. Considering how easily these facts are explained on the principle of reversion, there is a good argument for the assumption that all breeds are descended from Columba livia. There is in Columba livia, a still existing and widely distributed species which agrees in all manners of life and in structure with the domesticated pigeon. It breeds freely with them and produces fertile offspring. It varies in the state of nature between narrow limits. The most strongly divergent domesticated pigeons, i.e., carriers and short-faced tumblers, can be connected with the parent species by graduated differences not greater than those between the various varieties of "toy" pigeons. These differences are mainly in color and must be attributed to variation.

conditions have favored the modification of pigeons by selection and the written history of this modification dates back to the Egyptian dynasty of 3000 B. C. Biblical references are found in Genesis, Leviticus and Isaiah. Pliny wrote of the high regard in which fancy pigeons were held in ancient Rome. In 1600 Ahber Kahn had extensive aviaries in which were housed seventeen distinct breeds. By 1600, too, the Dutch were as interested in pigeons as the Romans had formerly been. In India, China, and Persia pigeons abound and have been carefully bred. All this care which has been

lavished throughout the ages has undoubtedly let to the perpetuation of variations.

Aldrovandi described Pouters before 1600. In 1735

Moore in describing the desired specimen said that seventeen
to eighteen inches was a good body length and that the correct length of leg was six and one-half or six and threeeighths inches. Today the minimum standard* requirement
calls for a body length of eighteen inches and a leg length
of seven inches, so that not much variation has taken place
in the last two hundred years.

Fantails, as such, did not exist 200 years ago. When first introduced into England they came from India and were known as the broad-tailed shaker. They were vastly inferior in carriage to the English type. In 1677 Willoughby mentioned that fantails had 26 tail feathers, but in France they had as many as 42 tail feathers, while modern fantails average about 36 tail feathers.

The barb was introduced into England from Barbary at least as early as 1687 but was different from the present day barb, particularly in width of gape and stoutness of beak. So it is evident from these three examples that three hundred years ago the birds had not diverged so far from the original stock.

Manner of the formation of the chief races

It is evident that dove-cot pigeons are not subject to variation much more than is Columba livia. When, however, they are confined in aviaries and fed well they are subject to changes in structure. Their feet and organs of flight grow smaller and correlated to this is an accompanying dim* Standard of Perfection. Boston, published by Pigeon News

THE RESIDENCE OF THE PARTY OF T

carded, but before modern breeds were established, these sports would have been retained. Fanciers have deliberately altered the appearances of breeds by selection and this would be called methodical selection. Breeding to a hypothetical standard, which Darwin called unconscious selection has produced the modern jacobin which Aldrovandi would have difficulty in recognizing as the descendent of his birds. No fancier wants the medium bird, but all strive for extremes.

It may be asked "Did old time fanciers have present types in mind?" To this the answer would most certainly have to be the negative. Unconscious selection answers it all i.e., a little variation added to a little has evolved a vastly different bird. When these variations occurred the parents were neglected and thus the connecting links have disappeared. There is no extant connecting link between Columba livia and the modern pouter but the Java fantail does serve as a connecting link between Columba livia and the modern fantail.

Prepotency in transmission of characters.

In Darwin's (1868) work with reciprocal crosses between pouters and fantails he found the pouters were prepotent.

He also found that barbs were prepotent to fantails and decided that this was probably due to the weakness of the fantails rather than to the strength of the other breeds. He found one exception in a case wherein a fantail was prepotent to a laugher.

Trumpeters, as a distinct breed, have been known for more than two hundred years and yet they are notoriously weak. They are characterized by a "rose" over the beak,

with the control of the second of the second

a crest on the head, feathers on the legs and a peculiar coo. Darwin crossed both sexes with turbits, almond tumblers, spots and runts then recrossed these mongrel offspring. As is common with other varieties, the crest and feathers on the feet were inherited but there was no vestige of the "rose" or of the peculiar coo. In opposition to Darwin's findings Neumeister wrote that in Germany such hybrids both trumpeted and had the "rose". Darwin imported a pair of these mongrels with the crest but never heard them trumpet. He crossed back these mongrels to trumpeters yet the "rose" did not reappear until the fourth generation. When the hybrids contained fifteen-sixteenths trumpeter blood they still did not trumpet. Darwin considered this a good example of the difference between heredity and prepotency for here is an ancient breed which breeds true, yet cannot transmit its two chief characteristic properties to its hybrids.

Darwin found another proof for his theory of a common ancestor in the fact that certain characteristics are inherited at corresponding periods, thus almond tumblers do not attain the full color and markings until after the third or fourth molt. This is true particularly of the males, for the female never becomes as dark as an adult male and the young bird, after the first molt, bears but slight resemblance to the adult male. In mottle and rose-wing tumblers the young, in their nest feathers, are invariably "self colored". Grizzle dragoons do not attain the correct color until two or three years of age.

Much interesting work has been done on the question of fertility as it is affected by domestication, inbreeding and outcrossing. It is not known whether the semi-domesticated

THE PARTY OF THE PROPERTY OF THE PROPERTY OF THE PARTY OF

dove-cote pigeon is more fertile than Columba livia but Darwin (1868) asserted that the domesticated pigeons are much more fertile than the dove-cote pigeons. It is apparent that domestication lengthens the breeding season and careful selection has resulted in such breeds as the white king which will raise ten broods in twelve months. An interesting fact noticed by several investigators is that dove-cote pigeons seem to have an aversion against mating with domesticated pigeons. There seems to be a general opinion that inbreeding leads to sterility and that an occasional outcross is necessary to restore fertility. The answer to this seems to be careful selection. By this method, size, vigor, and fertility may be retained indefinitely. The largest guinea pig on record was produced through inbreeding and very careful selection. Changed living conditions affect fertility, for Columba migratoria, a native of North America, in the wild state lays two eggs but in Lord Derby's aviary never laid more than one egg. The same fact has been observed with Columba leucocephala.

Darwin cited the curious case of correlation between the feet and the wings of the so called muffed breeds, i.e., breeds having feathers on the legs. These feathers differ from those on the grouse in that they resemble the primary flight feathers. In these muffed pigeons the two outer toes are connected by the skin and they correspond with the third and fourth toes. In the wing of the pigeon the first and fifth digits are aborted, the second digit is rudimentary and carries the so called "bastard wing", while the third and fourth digits are united and enclosed by skin. These latter together form the extremity of the wing. Not only does the

exterior surface of the toes support a row of feathers, like primaries, but the same digits which, in the wing are united by skin completely become partially united by skin in the feet. This is explained by the law of correlated variation of homologous parts. In such breeds as dragoons in which the wattle is large there is a correlated increase in size of the eye cere. It seems like working toward a hopeless goal for fanciers to try to increase one and simultaneously decrease the other.

Origin and history of color pattern

Charles Otis Whitman (1919) did valuable work in tracing the origin of the color pattern of Columba livia. He found an ancestral mark in Turtur orientalis and described it as a dark spot filling the whole central part of the feather, leaving a narrow distal edge of light color. The checker of Columba livia is shaped differently and has a lateral position. It appears in pairs, one on each side of the feather. To effect this grouping in pairs the pigment disappears from the tip of the feather and then along the shaft more rapidly than at the sides. However, in many checkered rock pigeons the inner feathers of the bar have undivided spots which gradually change into typical checkers on the lower end of the bar. There are many transitional steps which connect the ancestral type with the derived type and so demonstrate that the two marks are not separated by mutation gaps.

In listing these transitional steps Whitman described the three stages of the checker in the passenger pigeon.

He found the greatest variation in the checkers of the adult males, then of the adult females and, among the young, which

are nearly alike in both sexes, he found recapitulation of ancestral conditions. On the secondaries of the adult female he found a homologue of the posterior bar and on the first row of the long coverts he found a homologue of the anterior bar of Columba livia. The process of obliteration, however, is in progress over the entire checkered area and particularly in the anterior part of the wing. Thus, the checkers have rounded tips, the posterior bar is emarginated and the number of checkers is reduced by one half, some being mere spots. Whitman was just as sure that the obliteration was going on posteriorly as he was that the male represented an advance over the female while the latter showed an advance over the young.

The significance of the foregoing lies in the fact that it is not an isolated case, for the mourning dove Zenaidura carolinensis is a parallel case, but goes further as does Melopelia leucoptera. Here the adults show no checkers, but in the juvenile pattern there are a few vestigial spots on the last two rows of the long coverts, where the bars are usually best developed in the checkered patterns. Even in the adults, under the coverts and scapulars there are distinctly outlined areas, without pigment, which correspond to checkers.

The direction of evolution in Columba livia has been from a condition of relative uniformity to one of regional differentiation. Brown rather than gray was the primitive ancestral color. Gray is an effect produced by the withdrawal of brown pigment from the superficial parts of the feather and by the segmental arrangement of the pigment in the barbules. The fact that brown occurs in the plumage of wild species, also

in the juvenile plumage of birds, which in the adult plumage are gray, is evidence that brown represents the more primitive color.

Whitman (1919) gave the following description of a sparsely checkered Columba livia. The spots were longer and more pointed behind than on a gray bird. The posterior bar was most developed and, passing anteriorly, the spots were less and less developed. The posterior bar seldom showed the serrate edge while the second bar showed all stages of serration, the less black there was in the wing the greater the serration. In the juvenile plumage of domestic doves the second bar is most pointed and it becomes more so toward the outer portion of the wing. In the passenger pigeons there are well marked serrate bars in the juvenile plumage and in adult females. The young of the Geopelia have pointed bars which do not occur in the adult plumage. The fact that pointed bars are so widely distributed among wild pigeons shows that this is the archaic form, although in wild pigeons the bars are not limited to two as they are in Columba livia.

The patterns of most interest are the neck marks and the dark centers and pale tips. In Turtur turtur and Turtur orientalis there occurs no sign of the neck mark in the juvenile plumage except that from three to five rows are better defined as rows than the rest. In the blond ring dove, Streptopelia risoria, which is an advance over Turtur orientalis, more than half the birds possess plain lateral spots. In the related red ring dove, Streptopelia humilis, all the young possess these spots, this species having more pigment, hence enough to appear in the first feathers. In the Japanese ring dove, Streptopelia douraca, these spots appear.

Here is a good example of a character which occurs earlier in ontogeny than it does in phylogeny, i.e., what first appeared in the second feathers now appears in the juvenile feathers.

In Turtur orientalis the dark centers nearly fill the entire feather. This black center consists of a larger upper half and a smaller lower half, which asymmetry appears in the black spots of Columba livia. In the young the dark centers sometimes show brown but in the adult they are black and more pointed. Turtur turtur shows the black center reduced and more pointed. The anterior part of the wing has suffered the greatest reduction of black. The old types reach adult plumage conditions in their first plumage and among this number is Turtur turtur. In Spelopelia suratensis the black is still further reduced to a mesial stripe and it has bifurcated neck feathers. In Spelopelia chinensis even the mesial stripe has disappeared and the neck feathers, tipped with white, are bifurcated.

Whitman (1919) showed two methods of reducing the dark centers: first, by the guinea mark splitting the center into paired checkers and second, by reducing the center through an extension of the whole of the pale feather border. Evidence that this second method has occurred in the turtle doves is offered by the hybrids. When Turtur orientalis is crossed with the blond ring dove the indications of dark centers, in the young, are confined wholly to the shafts. The reduction process has not only wiped out the spots but has advanced from the dark red color to gray, isabelline, blond and finally to pure white (Streptopelia alba). Thus albinism is the finishing stage in this reduction process.

In a seven weeks old common pigeon Whitman found an oblique streak in which the feathers were gray without any brown. All the other feathers showed brown. Also he found a pure gray streak along each edge of the scapulars, which disappears in adult plumage for the whole wing is of that color.

The sequences appear to consist of discontinuous stages whose connecting phases seem to be lacking. This seems to fulfill the requirements of the mutation theory, but the phyletic series may be continuous, although the ontogenetic series is so rapid that relatively few stages appear on the surface. By plucking feathers in nestlings these phases may be brought to light. By varying slightly the time of plucking, by working on many different patterns and in several regions of each pattern, nature will show that it is not mutation but the law of genetic continuity that underlies the phenomena of colors and patterns in successive plumages. Whitman said that the intervals between stages are not periods of rest but of active progress in transitional elaboration. He said that the visible stages and the invisible flow of transitional, latent phases form a continuum which is analogous to the rhizome with its visible nodal growth arranged in serial order but appearing as isolated generations, because the inter nodal connections lie hidden beneath the surface of the soil.

In the oblique tract two or three rows of coverts appear two weeks later than the others, but the time varies for the different species. In the domestic pigeon, if the adult plumage is to be black, this streak will be blacker than the other coverts but not so black as in the adult plumage.

Since the first molt leaves this tract intact, it will still be recognizable but now from a deficiency rather than from an excess of black. This streak shows better in wild species where the adult plumage differs greatly from the juvenile stage. particularly in the ground doves of Australia, genus Geopelia. This genus includes four species. Whitman arranged them in the order of their respective stages of development as follows: (1) Geopelia tranquilla, with narrow white and black bars running entirely across the front of the neck with no median interruption. (2) Geopelia striata, with bars interrupted in the middle of the neck by a median streak of pale vinous. (3) Geopelia humeralis with no bars on front of neck. (4) Geopelia cuneata, with no bars on the front of the neck and the bars elsewhere transformed into spots. Numbers one, two and three all have the adult plumage on the wings and back edged with black. This group of Australian doves furnished Whitman with one of the best demonstrations of recapitulation that he discovered. In the ontogeny of the Geopelias the various species all arose from a common color pattern, consisting of longitudinal spots or checkers, distributed uniformily to all feathers of the wing. This common pattern is retained only a few weeks and the adult patterns diverge widely in two directions.

The turtle dove neck mark is not lost in the common pigeon for, if the neck feathers be lifted, their bases are seen to be dark. Whitman quoted from the Mustertauben Buche of Gustav Prutz who said that when self colored birds show differentiation in the plumage, they always show this differentiation in the same places as does the blue rock.

Whitman said that the pigeon unit of pattern is also the avian unit of pattern. In the young of the robin it is always present even if discoverable only through the use of a lens. Also it is found in the flicker, sandpiper, splendid parrakeet, black backed hemipolle, the collared plain wanderer, the curlew, the Phillipine rail, the Virginia rail, the wood sandpiper, the widgeon, the crowned guinea fowl and the ring necked pheasant of China. In Phaps chalcoptera, the bronze winged pigeon, there is a very much reduced black checker upon which is a brilliant irridescence. This, Whitman felt, is the beginning of the ocellus of the argus pheasant. In polyplectora biculcaratum the female retains the dark centered pigeon pattern while the male has more ocelli and those are irridescent, but have a brilliant black border surrounding each ocellus. In the bronze wing pigeon there is a similar black border on the terminal end of the spot, which gives it the ocellate form.

Whitman listed, as another example of recapitulation, the apical mark, which looks like lacing and appears only in the juvenile feathers. It is common to practically all pigeons although more plainly visible in birds with the color pattern of Columba affinis. The mark is crescentic in form, one half millemeter to one and a half millemeters wide at the shaft line in the larger coverts. It is broadest in pigeons of the Columba affinis type and becomes progressively narrower down through the barred type until it reaches almost the vanishing point in the so called self colored breeds of domestic pigeons. Since Whitman had already discovered a tendency to lose spots and checkers, he began to realize that the apical crescent was a thing "of history and destiny". In Turtur orientalis this

apical crescent shows at full width in the juvenile plumage and it persists throughout the adult life.

Determination of sex

From the time of Aristotle there has been much speculation regarding just why and how any particular animal should be of a particular sex. Darwin (1868) wrote of the prevailing idea that in a bisexual clutch of pigeon's eggs the first egg produced a male and the second egg a female. He. however, gave no satisfactory data on the question. Whitman (1919) crossed pigeons of related genera and arrived at the following conclusions: first, that there was a long term of life in the offspring; second, that practically all of the eggs developed; third, that there was a predominence of males from the eggs of the spring and early summer and from uncrowded clutches generally. He said that the two eggs of the clutch from pure females had different sex tendencies. If there was only one egg in a clutch it, apparently, was not subject to the influences of overwork, early season and crowded clutches. When these hybrids were mated back to their parents, there was a noticeable lessening in fertility, the young had a shorter term of life, the sex of the young bore no relation to the sequence of the eggs in the clutch and was independent of the season. Eggs from matings of complex hybrids were more fertile than eggs from matings of the first filial generation inter se or from the first filial generation with the parent species. Their expectation of life was longer but not so long as that of the first filial generation itself. The further breeding of first filial hybrids and of complex hybrids produced a high percentage of

intitle service out, on an orange of the continuent of the property one

abnormal young and of hermophrodites.

The crosses of Streptopelia alba with Turtur orientalis gave fifty-nine dark and forty light birds. The sex of forty-five of the dark birds was known and they were all males, while forty of the white birds were known and they were all females. The reciprocal crosses gave no white young but the males were lighter and the females dark. This is an interesting case of sex color linkage. Whitman said that, when different families or sub-families are crossed, the progeny will be male only, but if one parent is a hybrid the young may be produced without sex glands.

To support his statement that in breeding pure breeds the first egg will produce a male while the second egg will produce a female. Whitman cited Stigmatopelia senegalensis in which he found eleven males and two females from the first egg and nine females with two males from the second egg. Riddle (1916) corroborated Whitman's findings regarding the sex ratio, the effects of over work, old age and lateness of the season. He went further than Whitman, however, for he found that the first egg of a pigeon's clutch had a smaller yolk than did the second egg. There upon he came to the conclusion that pigeon's eggs are dimorphic. In some clutches both eggs had yolks of the same size and if both yolks were small both young would be males, but if both yolks were large both young would be females. He also found that old females laid eggs with larger yolks and that eggs laid late in the season and which produced females had larger yolks than those which were laid early in the season and produced males.

Living cells, in general, dispose of ingested food by

storing it or by oxidizing it and the products of oxidation, being removeable, do not increase the size of the cell. Thus the egg with the low storage capacity and small yolk is likewise the egg with the high oxidizing power and a greater percentage of water. As a result of the chemical analysis of eight hundred eggs Riddle came to the conclusion that low storage, high water content and high oxidizing power tended to produce males and he found these conditions present in eggs of early spring, the first egg of a bisexual clutch and eggs from mature, young, vigorous hens. If this higher metabolism exists in male producing pigeon's eggs and this is associated with higher water contest it throws light on several procedures employed to control the production of sex. Miss King in 1912, desiccated toad's eggs and obtained eightyseven percent of females. On the other hand, Hertwig and Kuschekewitch by "over ripening" frogs eggs (i.e., permitted them to absorb water) obtained one hundred percent males.

Riddle explained Whitman's work with wide crosses, which produced males, on the basis that heterosis gave greater vigor, hence higher metabolism. He also used a bomb calorimeter to show that eggs with larger yolks had a higher calorific value than eggs with smaller yolks. Turning to anatomy he observed that in pigeons, the right ovary begins to degenerate before hatching and is wholly absent from the week old squab. In squabs from over worked parents the right ovary tends to persist. He found this to be particularly true in the autumn and considered that it showed a tendency to produce females then.

In Mendelian phraseology, the female pigeon is heterozygous for sex. This means that dimorphic ova are produced

by the female and that selective fertilization is impossible. Since both sizes of ova are produced throughout the year there could be no selective elimination in the ovary. Riddle (1916) assumed that there might be a differential maturation, but to accept this it would be necessary to assume the elimination of an X-chromosome from one half of the ova in the spring and. the retention of this same X-chromosome in the homologous eggs of the autumn, the elimination of a Y-chromosome from the other half of the eggs laid during the autumn and the retention of all these Y's in the homologous eggs of the spring. To account for the several grades of females it would be necessary to postulate the fractional elimination of parts of the Y-chromosome, larger and larger parts being eliminated during the progress of the season. Riddle assumed that these postulates were ridiculous and therefore he believed that his theory of sex, due to differences in metabolism, was the correct explanation.

L. J. Cole (1916) recorded the sex of the young from approximately seventeen hundred clutches and came to the conclusion that the sex ratio is one hundred five to one hundred. Furthermore, he was unable to determine that the first egg of the clutch was more often a male.

At the beginning of the twentieth century biologists believed that an egg was completely ambivalent regarding the future sex of the resulting zygote. It seemed that environmental conditions either pre-natal or post-natal determined the sex of an animal. Crew (1927) in refuting this idea cited the case of the nine-banded armadillo in which all the litter arise from a single ovum and all are of the same sex. On the other hand, in animals where the different

CONTRACTOR CONTRACTOR SERVICE DESCRIPTION OF THE RESERVE OF THE RE at the office them a splitting the state of the same and state of the embryos arise from separate eggs the young are of both sexes. Now if sex depends on environment there is no reason for such a condition. The phenotypic differences by which males are distinguished from females are associated with constant differences in the chromosome content of the cells of the two sexes. In the somatic cells and in the immature gametes of the female pigeon the chromosomes are arranged in pairs which are morphologically similar except in one case. In the male, the members of this pair are, as is the case with all other pairs in both male and female morphologically alike. Since the tissues from males and females differ chromosomally only in this respect, this pair is called the sex chromosomes. In the male both are alike and they with the one in the female which is morphologically similar are known as the X-chromosome, while the dissimilar one in the female is called the Y-chromosome. Thus in the male pigeon the sex-chromosomes are XX, and the female XY.

At fertilization there will pass into each ripe gamete one sex chromosome from each pair. All sperms are alike because each contains an X-chromosome but there are two kinds of eggs, one containing the characteristic number of autosomes plus one X-chromosome, the other the same number of autosomes plus a Y-chromosome. When egg and sperm unite there will be two forms of zygotes, one that received an X-chromosome from the egg and another that received a Y-chromosome. The first will be XX and a male, the other XY and a female. This sex determining chromosome mechanism yields results comparable to those obtained when a heterozygous dominant (Aa) is mated to a recessive (aa) in a typical

The state of the s THE RESERVE ASSESSMENT OF THE PARTY OF THE P Mendelian monohybrid mating, i.e., equal numbers of the two classes that were represented in the mating. This would be what Crew would call the primary sex ratio.

crew (1927) said that the primary sex ratio will be equality if the two forms of gametes elaborated by the digametic sex are produced in equal numbers, or if the two forms are equally viable and functional or if fertilization is at random. He answered Riddle's theory that sexes might change by saying that the only possible explanation of the excess of females is that which postulates that the conditions of the experiment were such as to force the X-chromosome to pass into a polar body at the time of the reduction division more often than to remain in the egg.

Regarding Whitman's and Riddle's assertion that crowded clutches produced an excess of females Crew interpreted this as due to the fact that the production of one kind of gamete is physiologically more expensive than that of the other kind. If the demand for the elaboration of gametes is a tax on the reproductive system, then the kind of gametes that may be elaborated more easily will be elaborated in greater numbers. The alternative would be that the type which requires the greater physiological tax would be roughly made and thus lose out in the struggle for existence. It is the X bearing gamete of the digametic sex that is lacking either in number or in physiological perfection so, the over worked female pigeon produces more Y bearing eggs and hence more females. Crew also said that the differential production of gametes may be characteristic of a particular individual or strain, the result of some inherited mutation affecting the maturation division of the egg. On the other hand a disturbed primary

sex ratio may be due to a differential attraction for the sperm by the X and Y eggs of the heterogametic female.

In 1926 Crew placed two genetically dissimilar cocks with six hens. The great majority of the offspring claimed male A as their sire. The two males were then placed apart each with six hens for ten days, until they were laying fertile eggs, and then the males were interchanged. The influence of male A endured for nine days and that of male B for five days only. Crew interpreted these results on the assumption that the sperm of male B became stale, i.e., lost their vitality more quickly than did those of male A.

Riddle in 1924 recorded the complete sex reversal of a female turtle dove while Crew (1927) recorded that of an orpington hen. In both cases this sex reversal was due to tuberculosis which destroyed the ovarian tissue. All the foregoing evidence leads to the conclusion that sex is irrevocably fixed at fertilization.

Lace or Silky

The first written record of silky or laced pigeons occured in a treatise by an anonymous author in 1765. Since then laced fantails have been bred by fanciers but have never become particularly popular. It has been assumed that silkiness is a recessive sex-linked character. If such be the case the following conditions must result from reciprocal crosses in the first generation.

Laced male x normal female should produce normal males and laced females.

Homozygous normal males x laced females should produce normal offspring of both sexes and no laced birds.

In the actual breeding experiments recorded by Steele

tien and the course or min to seeps are sent bett

mated to laced birds. Group two, males homozygous for silkiness mated to normal females produced normal males and laced females—a typical case of criss—cross inheritance. Thus the groups one and two meet the requirements listed above. In the group three males heterozygous for normal were mated with normal females and produced normal birds of both sexes and laced females. In group four males heterozygous for normal plumage were mated to laced females and they produced normal and laced birds of both sexes. These results confirm the belief that laced or silky plumage is recessive to the normal plumage and that it is sex linked in its inheritance.

Laced pigeons are not bred commonly by fanciers because they are low in fertility and lack vigor. This, added to the fact that they do not fly readily, thus becoming an easy prey for vermin, accounts for their unpopularity.

Number of Tail Feathers

Ordinary pigeons have twelve tail feathers but there are occasional variations. Ivar Johansson, examined 1891 specimens to count the tail feathers and made the appended table.

			All the second of the second o					
No.	of	tail	feathers	101;	No.	of	pigeons	3 1
11	11	11	tt-	11 !	11	11	11	5
ff	11	11	tt	12 !	tt	11	11	1799
11	11	11	- 11	13 !	11	11	11	60
tt	11	11 11	tt	14 !	11	11	11	26
							-	1891

Thus it will be seen that pigeons with less than ten tail feathers are very rare and nobody has been able to discover

miletan remort and the party of the both to the terms

that lack of tail feathers is inheritable. There is, however, genetic relationship when the number of tail feathers is more than twelve. Eighty-six birds showed supernumary tail feathers. Of these fifty-two trace back to one pair. A tumbler cock No. 32A which had twelve tail feathers and No. 3A a tumbler hen of which no count was made. Two of their young, 109B and 161B, when mated together, produced fourteen young and of these, eleven had twelve tail feathers, two had thirteen feathers and one had fourteen feathers. This young male with fourteen tail feathers when mated to two different females each of which had twelve tail feathers, produced two birds with twelve, four birds with thirteen and one bird with fourteen tail feathers. Two young from 109B and 161B, each with twelve tail feathers when inbred, produced one young with twelve, one with thirteen and one with fourteen tail feathers.

From these meagre data the conclusion may be drawn that parents with supernumary tail feathers have a tendency to produce offspring with supernumary tail feathers. There is no sex linkage, however.

The Uropygial Gland

The presence, in pigeons, of the uropygial gland is the normal condition and of the 1360 birds examined by Johansson, while there was considerable variation as to size and condition of the gland, only seven lacked it entirely. The normal condition is one gland with a single papilla, but in some there is a distinct median groove making the gland appear double while, in others, there are two separate and distinct papillae.

Johansson's records as to the presence of a double or

single uropygial gland are very indefinite but of the seven birds without glands, two show no ancestors without the gland but the other five all trace back to the male 32A in which the gland was very small and the papilla was rudimentary. Thus the strain which produced birds, minus the gland, was the same strain which produced birds with supernumary tail feathers. Of the seven birds, six were males but this was not considered significant for such was not the case in fantail crosses.

In 1913 two pairs of fantails were added to the experimental breeders. From a white male 1355A x a yellow female 1355A four offspring were bred. Three of these lived long enough to have their tail feathers counted with the following results, twenty-one feathers, twenty-three and twenty-nine feathers. However, none of these lived long enough to breed.

When pigeons with the normal dozen tail feathers were crossed with fantails the first filial generation had the following distribution of tail feathers.

No. of tail feathers	14	15	16	17	18	19	20	21	22	23	24	
No. of birds	4	2	2	2		2		1	2		1	Total

All these first filial birds, but two, had the uropygial gland and these two came from female 1208B which had but a rudimentary gland. The mating of female 1208B, which had thirteen tail feathers and a rudimentary gland, to male 1480A, which had thirty-one tail feathers and no gland, gave four offspring--two with the gland and two without, and the number of tail feathers was fourteen, fifteen, sixteen and seventeen. Thus, although both parents had supernumary feathers, the range

in the offspring was no greater than in the case of the matings between fantails and pigeons with the normal number of tail feathers. Morgan in his study of the inheritance of the number of tail feathers of the fantail pigeon found the range to be from twelve to twenty but at Wisconsin they could find no bird in the first filial generation with less than fourteen tail feathers.

Only two second filial matings produced young and of these one mating produced two young while the other mating produced sixteen. The parents both had twenty two tail feathers and the uropygial gland was present. In the appended table the number of tail feathers is given for only fourteen birds but the determination of the presence or absence of the uropygial gland was made in all sixteen young.

No. of tail feathers 14 15 16 17 18 19 20 21 22 23 24

No. of birds

1 1 1 2 1 1 2 1 1 2 14 total

Uro. Gland

4 + 0 0 + + 0 0 + 0 0

means normal gland - means small gland 0 means no gland

It will be seen that the range of variation is not greater in the second filial generation than it was in the first filial generation but the number of cases is very small.

There is a popular belief that there is a correlation between a high number of tail feathers and the absence of the uropygial gland. Although Morgan accepted this idea and said there may be a linkage between the gene for supernumary tail feathers and the gene for the absence of the uropygial gland, the

A back cross of the first filial generation to a normal pigeon gave seventy-five young from eleven matings. A table of these young is appended.

tables of Johansson's results do not bear out such a linkage.

No.	of tail feathers	12	13	14	15	16	17	Undetermined	Total
No.	of birds	33	12	14	6	2	3		75
U.g.	normal	18	4	8	5	2	3	5	45
11 11	small	12	6	5					23
11 11	absent	3	2	1	1				7

Here again we find no evidence of a correlation between supernumary tail feathers and the absence of the uropygial gland. Thus the results obtained from the first filial generation and from the back cross would seem to point in the direction of the independence of these characters. But it is apparent that the first filial birds with a high number of tail feathers are more apt to produce offspring with a high number of tail feathers than are first filial birds with a low number of tail feathers.

In a second back cross of the second filial generation to grade back the fantails it was found that eighty-four percent of the progeny had the normal twelve feathers. When the first filial generation was back crossed to the normal only forty-six percent had twelve feathers.

Thus it appears that non-genetic variation is greater toward the recessive (fantail) end than toward the normal end. The stock used by both Morgan and Johansson was apparently heterozygous for both factors. This may be explained by a possible cross of the tumbler, possessing the normal number of tail feathers and the uropygial gland, with the oriental roller which has supernumary tail feathers and no oil gland.

Color Inheritance and Breeding

In discussing color in pigeons it is necessary to bear in mind two facts. First, that the pigment is always present in infinitely small granules and second that there is

not a distinct color of pigment corresponding to all the different apparent colors, for color depends on the arrangement of the granules.

Metzelaar (1926), discarding the checker pattern arranged the intense colors in two groups, thus:

Barred Solid

Blue Black

Brown Silver Brown

Mealy Red

Each of these has its dilute color, thus:

Barred Solid

Blue Black

Silver Dun

Brown Silver Brown

Lavender Silver Lavender

Red barred (mealy) Red

Yellow barred (cream) Yellow

Metzelaar, for the first time, distinguished brown from dun. Lavender, the dilute of dun, is very rare but occurs in carriers.

Blue and black are made up of the same kind of pigment, i.e., black pigment granules. In blue these pigment granules are clumped together while in black they are spread out. In the dilute colors the pigment is only about one-third as abundant as in the intense color. Thus silver has one-third the amount of pigment as have blue and black. Dun, blue and silver are all formed by minute pigment granules arranged in different order.

In birds of the blue barred pattern the white rump is dominant, thus showing descent from the blue rock pigeon.

In India occurs Columba intermedia in which the rump is blue and if crossed with Columba livia the pure recessives would breed birds with blue rumps. If no blue rumps are at hand the same result can be secured by crossing in black or dun.

According to Van Hoosen Jones there are six gradations from black to blue. First, full black; second, checkered; third, sooty; fourth, blue; fifth, black barred; sixth, blue barless. The basic factor in this series is B (black pigment). The first group of factors consists of five which belong to a series in which the lowest is Ba (r.) It spreads black pigment in the region of the wing bars. Next is So(oty) which produces a sprinkling of black in the wing coverts; Third is the checkering factor (C); the fourth, T(ail) spreads black throughout the wing coverts leaving a blue tail; S(pread) is the highest member of the series and spreads black pigment throughout the tail, thus producing a full black. These are dominant in the order given and bear out Whitman's theory that the change from black to blue transpires posteriorly. Van Hoosen Jones said that no upper member can ever be produced by a pair lower in the series, that is, with less black. Thus two checkered parents can never produce a self. Criss-Cross Inheritance

Silver is dilute blue, i.e., clumped black pigment present in only one third the amount. Thus according to Metzelaar (1926) the fancier's much sought black barred silver is an impossibility, for the black in the bars must be diluterable. At one time it was the universal belief that all silver dragoons were female. Today male silvers abound and they can be produced thus. Mate a silver female to a homozygous blue and all the young will be blue. Mate one of

the warming to constraint and their an electricity death the contraint

these male young to a silver female and the colors will be equally divided irrespective of sex. Now if one of the silver males be mated to a blue hen the young males will be blue while the young females will be silver. This is the so called "criss-cross inheritance" in which, if the sire be dilute, the intensity of the parents is reversed in the sex of the young.

Metzelaar has been successful in distinguishing two kinds of red, i.e., dominant to black and recessive to black. If a red cock of the first type be mated to a black female the young will all be red, whereas, if the cock be of the second red type, the young will all be black. This second type is the more common and it remained for Metzelaar to point out the existence of the first type. Leon J. Cole (1914) has shown the complete dominance of black. In the first filial generation he bred one red in four. The extracted red often has a bluish rump. The recessive red never has clumped pigment even when the factors for clumping are present.

So called grizzle is caused by part of the barbs of the feather being white and part blue. It occurs typically in blue birds but silver and red checker grizzles are sometimes found in dragoons. Grizzle seems to exist only in the heterozygous condition and must be maintained by constant crossing with blue, to which it is dominant. When two grizzles are mated together the young will show an excess of white but when mated to blue the young will be fifty percent grizzle irrespective of sex.

Lacing

Lacing is the type of pattern farthest removed from the original pattern of Turtur orientalis. Lacing is "central

reduction of pigment" and the peripheral portion of the feather has the black unaffected. When this peripheral black is sufficiently narrow the bird is laced. Schietti modenas and oriental frills offer the best examples of lacing. If true black and red lacing is present the feather is red except for the peripheral section. Sometimes the black disappears from the edge and the bird is a self red as in mahogany modenas. Agents which control lacing act only on spread pigment, not on clumped pigment. Thus if a bird is fundamentally a blue, only the wing bars are red while if it is fundamentally checkered the checker becomes red and is called "spangling". In this case the red spots have black margins just as the bars have. Further along in the scale the red has become white and many red-laced birds show this central trace of white in the red spots. White laced birds are found in strassers. polish lynx, ice pigeons, starlings, monks, priests, suabians and modenas. If the central whitening is incomplete there is a white spot surrounded by two bands, first red and then black. This white is dominant to red and although the juvenile plumage may show red, the white will appear in the adult plumage. Metzelaar called the fundamental color on which the lacing has been superimposed the ground color. In the ideal condition the spread out pigment has been suppressed and replaced by white, except for the edging. Thus all lacing factors are centrifugal suppressors. The exterior appearance of a laced pigeon depends on the following factors: first, the fundamental color; second, the fundamental pattern, whether barred or checkered; third, the degree of completeness of lacing; fourth, whether the reduction has been to red or white; fifth, age and health.

White

There are at least three types of white. First is the pure recessive white and there are two whites which are both dominant to black. One is the final stage in the reduction of red to white and occurs, typically in the white tippler. The other represents the complete washing out of black. White is unfit for any crossing and hence white fancy varieties usually are inferior to other colors, structurally, due to a lack of a proper out cross.

Sex linked characters

The intensity factor I acts on both black and red pigment and the effect is to increase the amount of pigment by
three times what it would be if the I factor were lacking and
it affects pigment in all parts of the plumage. If pigment
is present a microscope will detect and determine the colors
readily but if the birds are white the colors may be determined only by breeding tests.

Cole and Kelley (1914) noted that in sixty-four cases, with only four exceptions, birds whose adult plumage would be intense had abundant "down" while birds whose adult plumage would be dilute had sparse "down" when newly hatched.

These exceptions are important for, if they are true exceptions, it would appear that an abundance of "down" depends upon a separate sex linked factor closely, but not completely linked to I. Darwin (1868) said, "Mr. Tegetmeir has informed me of a curious and inexplicable case of correlation, namely, that young pigeons of all breeds which, when molted, become white, yellow, silver, (i.e., extremely light blue) or dun colored, are born almost naked, whereas pigeons of other colors are born well clothed with down." Cole and Kelley (1914) re-

corded a certain kind of white which had a plentiful supply of down and hence appeared to be intense. In ring doves there is a parallel condition and it would appear that the difference between white and blond ring doves is a difference in intensity. The sex linked character which is responsible is probably homologous to the factor I in the domestic pigeon. Dominant red and gray

In the presence of the factor B the plumage color is black, blue, dun or silver while in the absence of B it is uniform red or yellow. This is the recessive red mentioned by Metzelaar (1926). A is a second factor capable of producing a distinct but not uniform red. If a bird, carrying both B and A be mated to a homozygous black the offspring are red. Hence this type is the dominant red to distinguish it from the recessive red (ba) previously described. The A factor, like I, is sex linked, the female never being homozygous for dominant red. On the other hand, the recessive red is transmitted in inheritance independently of sex. The primary characteristic of the A factor is that it modifies black and not that it produces red pigment. Cole and Kelley (1914) have produced a series of sex linked gray birds, dominant to black, by the use of this A factor. Red and yellow birds which carry A but lack B (females bAi and bAI) cannot be distinguished by their appearance from ordinary recessive red and yellow birds whose factors are bal and bai. A characteristic of all birds bearing both A and B is a "washed out" tail. This fact is useful in classifying white splashes.

Among pigeons which bear the B factor but lack the A factor there are three general types; uniform black, check and blue barred. There are, however, some variations within

each group. Thus black selfs may be dull or glossy. The check pattern may be light or dark. While the ground color may be blue or it may be "smoky". The barred types have two black bars on the wings and a broad bar on the distal portion of the tail. The rest of the wings and the contour feathers may be clear blue or smoky. Both the dominant red and the dominant gray series have types which correspond to the above. Birds in the red series, which would be black if they lacked A, have the wing coverts, head, neck and back of a uniform red, while there is a lighter color in the rump, belly, outer primaries and the tail. These light ones may be bluish or rusty brown. Red checkers also occur and are like the uniform dominant reds in that they do not show a tail bar. The type in this dominant red series which corresponds to blue barred in the black series is called silver and ash by homer fanciers. Cole and Kelley (1914) called them red barred. The tail bar region is commonly lighter than the rest of the tail. All that has been said of the effects of A applies to birds which lack I as well as it does to birds having it. A (BA) bird, lacking I, is yellow just as a red bird (ba) is yellow if I is absent. The dilute condition of the red barred (BsAI) is bluish or grayish with yellow wing bars. Cole and Kelley have identified the A factor in homers, white clean legged tumblers, white muffed tumblers, white fantails, and red bald-head tumblers.

Nuttall in his experiments, quoted by Cole (1914), found that red checkers were dominant to blue checkers and that the checker pattern was dominant to its absence. He assumed two sets of allelomorphs to account for the four color types.

These were R, presence of red; r, absence of red; C, presence

all fore-the brustiers and all the bear all all the said and

of checker pattern; c, absence of checker pattern. Thus RC is a red checker, Rc a mealy, rC a blue checker and rc blue. Cole (1914) said that Nuttall's red checker was the same as his dominant red and that Nuttall's mealy was Cole's red barred. Therefore Nuttall's R factor is the same as Cole's A factor but Nuttall was unaware of its sex linked nature.

Cole (1914) listed three types of matings which provided evidence of segregation. For the I factor there are seventyeight matings: male I x female Ii: expectation two intense males to one intense female to one dilute female. Seventy matings: male i x female Ii: expectation one intense male to one dilute female to one intense female to one dilute fe-Sixty matings: male I x female ii: expectation one intense male to one dilute female. He found no exception and so came to the conclusion that for the intensity factor T, in pigeons, there are no cases of partial sex linkage. The records reveal a constant excess of males and of intense birds beyond the expectation. In the experiments on the inheritance of the A factor there was an unexpected excess of females, but there was no explanation forth coming. The two factors I and A show a slight but appreciable mutual linkage. Crossing over in the males occurred in forty percent of the cases but in the females did not occur at all. Melanin pigments

The pigments which give their color to pigeons belong to the group known as melanins. These pigments are of a granular nature, have a definite shape and can be measured microscopically. It is thought that each animal has a granule shape of its own, for instance, the pigment granules in Columba livia are rod shaped.

THE RESERVE CONTRACT OF THE PROPERTY OF THE PR - CTT. DECEMBER CONTRACTOR STREET, STR

Since such specialized cells occur in developing feathers and since they actively form pigment, some workers in this field have ascribed the whole duty of pigment formation to them. In breeds such as the tumbler pigeons it is frequently impossible and it is never easy to establish the continuity of the cell processes. Any of the intermediate cells may form pigment and in tumblers all stages, from the specialized branching cells to those forming but a very few granules, are seen.

Red and yellow are perfectly distinct, for red is the intense condition while yellow is the dilute condition of the same pigment. This has been proved microscopically and chemically. In yellow pigeons the pigment is almost imperceptable in the barbules and in them the segmented condition of the pigment is seldom seen although hooked barbules may show it weakly. Because of this scarcity of granules the nuclear areas of yellow feathers are not so clearly marked out. Orren Lloyd-Jones (1915) said that he had never seen pigment in hooks or barbules. In yellow barbs the pigment is confined to the apex while the lateral sheets of the cortex and the medullary rays show no pigment. The particular difference between reds and yellows, however, lies in the nature and form of the pigment granules. In yellow feathers the pigment occurs as irregular, formless clumps. These clumps appear to be granular in nature but their exact shape cannot be determined by the use of a microscope. This is a distinct and constant difference between the pigments of red and yellow feathers. When dun, black or white feathers contain minute specks of reddish pigment it is necessary to determine the color, according to the above differences, by use of the

microscope. Yellow is produced by the same processes as red except that the final product is a shapeless mass instead of the distinct spheres of the red pigment.

Black is pure black and is not the effect produced by massing dark brown color material. In a black feather. places can always be found where pigment granules are so sparsely grouped that the individual granules can be examined. Chemical treatment also establishes the existence of black as a color per se. Black feathers contain much pigment and it is distributed in essentially the same manner as in red feathers. The hooked barbules have more pigment than do the curved barbules. The pigment occurs in well defined, uniform granules about one-half mu in diameter. Birds other than Columba livia have black pigment occuring in the form of rods from eight-tenths mu to one and one-half mu long and twotenths mu in diameter. The long axis usually lies parallel to the long axis of the barbule. If viewed in a cross section of the barbule these rod shaped granules appear to be shperical. Thus there are two distinct types of pigment which are similar in color, intensity and sheen. Usually these two types of granules appear in the same bird and then blacks may be classified as predominantly spheres or predominantly rods, although a few cases have been found where the two types were about equal. Of sixty-five black pigeons which have been studied in this connection, in none has the granular shape been found correlated with either age, sex or genetic constitution, for in the case of birds bearing both granular shapes one pigment cell will be found elaborating rods while the immediately adjacent cell elaborates spheres.

Dun is produced by the same pigment which produces black

so the difference is quantitative, but the pigment is more finely and uniformly divided. Thus, the granules of dun pigeons are two-tenths mu and spherical. The color in black birds may become so weak that it may be described as dun. This occurs more especially in the contour feathers on the side of the body and in the under wing coverts and is due solely to a reduction in the number of pigment granules, the black being diluted without the aid of a dilution factor. The body and wing coverts of blue pigeons may also show dun. Dun also occurs in the wing bars of silvers. Thus there are four kinds of dun, yet Lloyd-Jones called only one of them dun.

The so called blue in Columba livia is not the blue of the blue bird but is, in reality, a gray similar to the blue rabbit or the color of a maltese cat. It is nearest to Ridgeway's "gull gray" on plate fifty-three. The real spectrum blue occurs in some of the tropical members of the pigeon family. The pigment is the same as in black or dun differing only in the shape of the rods and in their distribution. the feather barb the pigment is restricted entirely to the apex. There is no pigment whatever in the lateral sheets of cortex or in the medullary cells. In black pigeons and in the true blue jay the medullary cells have much pigment which is over laid by cells and tissue which contain no pigment. In the barbule the pigment is massed closely together in the middle of each cell, not spread out through the cell. This arrangement leaves large areas for the reflection of light and if these regions are freely interspersed with regions which reflect no light, so called black areas, the effect is gray. Thus the blue effect is produced by a covering of pigment-free

keratin. The wing coverts of a blue pigeon are blue only in the distal part, the proximal end being dun if viewed from the dorsal aspect. If viewed from the ventral side the feathers are blue all over. The clumping of the pigment is broken down in the proximal parts but the pigment in the barbules has spread toward the dorsal recurved margin only. The ventral half of the barbule contains no pigment and is covered with a colorless layer of keratin. It is for this reason that otherwise good blacks show a bluish cast on the ventral side of the feathers and reds show ashy color on the primaries.

Blue pigeons show granules invariably spherical and larger than are ever found in blacks, being from eight-tenths to one mu in diameter. If the pigment masses are small and are not closely packed they may reach two mu in diameter. It has been definitely proven that pigment granules occur only in the epidermal layer of the feather.

The color which pigeon fanciers call red is, in reality, brown and the nearest color is Ridgeway's chestnut (plate two) or his pecan brown (plate eighteen). These brown granules transmit light and, moreover, are never clumped together closely enough to prohibit the passage of light. These granules are distinct clear cut spheres, typically three-tenths mu in diameter. The first sign of pigment formation in red feathers appears in the intermediate and inner sheath cells before the formation of the ridges. It may be either in or between the cells later, but before the ridge formation the clumps are denser and more numerous. Later, when the epidermal cells are cut up into ridges, each ridge encloses its share of pigment which is scattered in them and sends out

branches. These are the so called melanoblasts, melanophores or pigment cells and are most frequently found near the base of the ridge, but they have been found all over the inner sheath cells.

Some of the prominent workers in this field of malenogenesis were Stadelmann, Nencki, Schmiedeberg, Chittenden, Hoffmeister, Von Furth, Hopkins and Cole, Schneider and others. These men discovered that artificial melanins are the equivalent of natural melanins. Their search for the melanin chromogens led them to the discovery that tyrosin and its related aromatic compounds are the chromogens concerned. Then they had the task of determining how melanin was formed from the chromogen. In 1873 Hlasiwetz and Huberman discovered that oxidation was the process by which artificial melanins were made. In 1899 Landolt extended this theory to include the natural pigment of the choroid. In 1896 Bertrand found an oxidizing enzyme, called tyrosinase with which he was able to change tyrosin into melanin-like bodies. Since then it has been proven that these tyrosin-like ferments occur widely in both the animal and the vegetable kingdoms. They appear, practically always, when a physiological or pathological formation of melanin takes place.

In 1902 Dewitz, working with fly larvae (Lucilia caesar) showed how tyrosinase works in the skin of normal living and growing animals. He also showed that free oxygen is indispensable. He therefore concluded that there was, in the blood of the larvae, an enzyme which oxidized the chromogen and thus formed a brown or a black pigment.

In 1903 Gessard said that when tyrosinase oxidizes tyrosin it forms the black pigment that is formed in the physi-

ological or pathological development of melanin tissue. Moreover, he claimed that there thus arose a series of colors such
as rose and brown. The gradation in the color scheme depended upon the presence of acids, bases and salts.

In 1908 Bertrand determined the type of substance which tyrosinase may oxidize to form melanin compounds. these compounds passes through a series of colors before it reaches the final stage of oxidation. There is a slight variation in the exact tint of the initial and the final colors but the ear lier stages of oxidation give lighter colors, the series usually running from yellow to orange through the darker tints to brown and black. Bertrand's work showed that any benzene nucleus, with an attached hydroxyl, may be acted upon by tyrosinase to form a melanin pigment. The size and complexity of this lateral chain is of little importance for, unless it be too strongly acid or basic, it does not interfere with oxidation. Ethyl tyrosin, chloracetyltyrosin and glycyltyrosin were oxidized readily enough but they begin with yellow or orange and end with red or mahogany, thus missing the final stage, black. Thus it is seen that a single chromogen, acted upon by a single enzyme produces a whole series of colors, depending upon the degree of oxidation. twenty percent solution of tyrosinase tyrosin in ten minutes developed a rose color which, in from four to five hours, became black. Bertrand's researches and his results deny the principle of the absolute specificity of enzyme actions while the Mendelian interpretation of the same phenomena would demand a very high degree of specificity. In general the knowledge from pathology indicates that in the building of melanin the condition of the organism has so much influence that any

theory of "once for all determination" by shuffling color factors through the genes may be disregarded.

Spiegler, reported that he had found white melanin in horse hair and in sheep's wool. This represents, apparently a more advanced stage of oxidation than does the black color. In birds, on the other hand, white seems to represent the least stage of oxidation for, no pigment is detected and white seems to be a purely physical color.

Gustave Tornier, working with amphibia, performed some interesting and enlightening experiments on the control of color of the integument, through diet and the control of He used tadpoles and by controlling the diet nutrition. he produced a whole series of colors from white, yellow, red and gray to black. He found that he could do the same thing by coagulating the egg yolk so that the developing embryo had progressively less to eat. Moreover, he found that the same experiment could be carried in the opposite direction. These experiments would seem to show that in an animal which produces melanin there exists all the machinery necessary to produce a series or scale of colors. What color is produced seems to depend upon the physiological state of the organism and, in some well authenticated cases, the limiting factor has been the available oxygen or food supply. Riddle (1909) has been able to prove definitely in birds that the daily nutritive changes which accompany the low blood pressure periods which occur at night, influence the quantity of melanin produced. He said that "the specific color of an animal then is an index, not of the presence in the germ from which this animal rose, of certain chromogens and specific enzymes, and the absence of a wide series of others but this specific color means that a process with a wide range

of possibilities, because of a particular physiological state and environmental conditions, has struck this particular equilibrium. One and the same organism has within it all that is necessary to move that equilibrium up or down--taking the red, for example, we can in the words of Tornier "force it to black or white".

The "presence absence" hypothesis of the Mendelians rests upon the following quotation from Cuezot in 1903. "Again one learns that the authors who have recently studied the origin of melanin pigments, Biedermann, Von Furth, Scheider and Gessard, state that these pigments result from the action of an oxidizing enzyme (tyrosinase) upon a chromogenic substance; there are good reasons for supposing that things happen similarly in the pigmentation of the skin; there should be, however, in this case either two different chromogens and only one enzyme or only one chromogen and two enzymes, the one for the blackish pigment and the one for the yellow pigment. We adopt provisionally, for the convenience of language, this latter hypothesis.

The germ plasma of a gray mouse should contain potentially the three substances which by their reciprocal reactions later produce the deposition of pigment in the hair; and doubtless these three substances are contained in the potential state within many of the material particles of the germ plasma (representing particles or qualitative substances of the egg-mnemons). In a gray mouse (black and yellow pigmented) there are three mnemons, one for the chromogen and two for the two ferments; in a black mouse there are only two mnemons, one for the chromogen and another for the formative

enzyme of black pigment.

In regard to albinos, all is explained if we admit that their germ plasma contains only the mnemons of the enzymes, that of the chromogen being totally absent. With these conditions colored hair cannot be formed in albinos, since one of the substances indispensable to the reaction is absent, but one easily understands that the albino will transmit to its progeny either the mnemons for two enzymes, or one mnemon only, if it possesses but one."

The facts regarding the origin of melanin which have been discovered in various laboratories are diametrically opposed to this theory of Cuezot. It has been definitely established that one and the same chromogen produces both yellow and black and that the one ferment, tyrosinase, will produce both yellow and black from the same chromogen. It is now known that tyrosin and its related compounds are chromogens which occur, in the animal world, practically wherever protoplasm occurs. Thus the absence of melanin chromogen in albinos is practically inconceivable. Hence, according to Riddle (1909), it is absurd to postulate the formation of chromogen and non chromogen bearing gametes. He also said that an albino mouse must eat in its food every day large numbers of chromogens. Thus it would have melanin chromogens even if they did not come in by way of the gametes. This fact, in Riddle's judgment proves conclusively that Cuezot's hypothesis is highly untenable.

Usually in animals yellow color has been found to be recessive to other color, but in mice it has been proven that yellow is a dominant color. This fact has puzzled Mende-

lians and Riddle suggested that yellow, in mice, is a blend. Castle in 1906 reported that he had secured yellow mice from two sources, i.e., from a yellow male x a chocolate female, an albino male x a chocolate female. Each of these crosses has one color more oxidized than yellow (yellow, chocolate, black, albino) and one less oxidized than yellow. Thus the yellow here produced is a blend. More evidence that yellow is a blend is found in the fact that all yellow mice are heterozygous for yellow. Thus we see that yellow mice have the power to oxidize tyrosin compounds to an intermediate point.

Cuezot. Bateson and others attempted to explain color inheritance on the theory that recessives altogether lack the factor for color production. Castles refuted that theory because he found that the same pigment which is present in dominants is also present in recessives. He attempted to explain this condition on the basis that although all the factors were present, some inhibit the activity of others, i.e., he postulated the theory of activity and latency. Riddle said that we must take the next step and assume that in color inheritance there are mixed varying powers to oxidize tyrosin. The environment conditions plus the conditions supplied by the differentiation of tissues and organs supply whatever else is necessary for the process of color production. Castle showed that there is no such thing as total absence of characters for he says that purity of gametes does not exist and, further that purity of factors does not exist. This may be construed as a pretty definite proof that factors themselves do not exist but are, rather figments in the imagination of the Mendelian disciples.

Bertrand and Gessard have shown that if a parent is to

transmit the enzyme for black it must, at the same time, transmit also the enzyme for the whole series of colors, such as brown, chocolate, red, yellow, etc. without the absence of any one. Now if we admit the Mendelian conception that each of these factors may be transmitted according to the laws of chance, how often may we expect pure bred black parents to produce black offspring; Tornier could, by manipulating the diet of an animal possessing black enzymes, make it produce colors of a lesser degree of oxidation. So the black producing enzyme failed to produce black in that case.

In color inheritance, when two pure colors are crossed there are four possible results; first, the tyrosin oxidizing power of the male cell is established either immediately or in the succeeding generations, throughout the fertilized ovum and its derivatives; second, the tyrosin oxidizing power of the female may be so established and these would be the "dominants"; third, the tyrosin oxidizing power resulting from the union is either greater than or less than that in either of the gametes; fourth, the result of the union may be a blend, i.e., the oxidizing power may be intermediate between that of the two gametes.

SUMMARY

In the foregoing list of material which has been gathered from the works of the various authors studied there are, apparently, several very serious contradictions and differences of opinion.

Darwin was a most painstaking observer and a keen critic, as well as an indefatigable worker. He dipped into so many kinds of animal life that it is remarkable that he was able to treat any one as exhaustively as he did pigeons.

As a pioneer he did not have at his command the many controls and tools that the present day investigators have at their command, yet his observations of the skeletons of the various breeds of pigeons led him to the belief that the gap between the short-faced tumbler and the long-faced English carrier could be bridged by the differences in all the intermediate breeds. He substantiated many of his claims by the results of his breeding tests. Both Darwin and other investigators believed that the races of wild pigeons offer a better field for experiment than do the domesticated pigeons.

An insurmountable obstacle between Darwin's work and that of the present day investigators is this. Darwin claimed that the blue barred pattern is the original plumage pattern and, incidentally, he recorded having bred a checker pattern from two blue barred parents. Now the theory of Whitman, Van Hoosen Jones, Lloyd-Jones, Metzelaar, and indeed all present day investigators is that it is impossible to breed a checker pattern from two blue barred parents. They believe and, apparently, have proved that the direction of evolution has been from black to blue and that it is impossible to breed a higher member of the series from two parents lower in the scale. This is an insurmountable difficulty because Darwin was an exacting critic and an accurate recorder. On the other hand, Whitman, equally exacting and just as careful, failed in seven years of experimental work, to find a checker bred from two blue barred birds. One possible solution suggests itself, which is, that Darwin recorded the plumage pattern of his bird before it was fully feathered because it failed to live to maturity. Since he was already convinced that the blue barred pattern

was the original he would not be on his guard against such an error.

Whitman did much more painstaking work with plumage patterns and he went further than did Darwin in that he traced the pattern down to the original, which he claimed to have found in Turtur orientalis. He went even further and discovered the fundamental pattern in robins, rails, etc. He advanced more and better arguments for the theory that all our domesticated pigeons are descended from a common ancestor than did Darwin. Today it would be a particularly obstinate man who would deny this hypothesis. Having accepted the hypothesis of a common ancestor, the next step is to trace the steps by which the growth has come about. This offers a fertile field for the followers of Mendel. Without the aid of other weapons than a fertile imagination they have postulated "factors" which are transmitted with the genes. Highly hypothetical as this may seem, their theories have been substantiated by most exhaustive breeding tests. Men like Cole and Metzelaar have performed very carefully controlled breeding tests and their factor hypotheses have explained the results. In his interesting papers Metzelaar paid particular attention to modenas. In a letter written immediately preceding his untimely death Dr. Metzelaar said, in part, "--that I have been able to confirm my expectation that the bronze color of a bronze tippler or dark archangel and the mahogany of the spangling on the modena wings only differ from each other in minor respects. The bronze tippler has the spreading factor S1, which the modena lacks. Now in as much as archangel or tippler bronze can be diluted to golden by the presence of a dominant diluter D it is possible to

- Drope through the transmitted the total and the second transmitted the second transmitted to the second transmitted to the second transmitted transmitted to the second transmitted tran

combine this D with bronze spangling or lacing in the absence of sl and thus obtain a whole new series of colors like this: black, golden barred brown golden barred black, golden check brown, golden check

blue, golden barred brown silver, golden barred blue check, golden spangle brown check, golden spangle black, golden laced brown, golden laced

I am now working at the problem of materializing all these new creations and get a complete set -- ."

Whitman had statistical proof regarding the sex ratio and the effect of early season, crowded clutches, age of the parents, and the width of the cross upon the sex of pigeons. He had not, however, a satisfactory explanation of why these conditions occurred. Riddle accepted Whitman's findings and endeavored to explain them on the basis of metabolism. His theory that the first egg of a bisexual clutch would be the male because it had a higher power of oxidation listed the effect rather than the cause. Cole's statistics regarding the sex ratio tend to cast serious doubts on Whitman's findings and Riddle's explanation. The work of Crew and other present day investigators, on the chromosome would seem to have established definitely the fact that sex is irrevocably determined at the time of fertilization and that all subsequent influences are null and void. So the higher oxidizing power of the male producing egg is but a result, not a cause, of sex determination. Crew reported the complete sex reversal of a buff orpington fowl and Riddle reported as similar instance in the case of a turtle dove. These reversals were shown, at autopsy, to be due to tuberculosis of the ovarian tissues and were therefore, not pertinent to the subject

of sex determination.

It is a long step from the breeding pen in the experiment station to the test tube in the laboratory. Yet the next step is just that. Men who have never conducted breeding experiments with pigeons have been able to determine the ingredients of melanin colors and to determine the enzymes necessary to change the pigment in a chromogen to a whole series of colors. Riddle went so far as to say that any bird which carries chromogens also carries the mechanism for the potential manufacture of the entire series of colors. He scoffed at the Mendelians with their hypothetical factors, yet he did not explain why one color is produced and not another in the series. He could tell how a color is produced but not why. Each of the methods of approach to this problem of color breeding has produced valuable material for the geneticist but it would seem, from the results secured, that the method of chemical analysis and microscopic investigation offers the most fruitful field for the future investigators.

BIBLIOGRAPHY

- Darwin, Charles (1892)
 "The Descent of Man"
 D. Appleton and Company 1892 New York, Second Edition
- Darwin, Charles
 "The Origin of Species"
 Thomas Y. Crowell and Company
 New York
- Darwin, Charles, M. A. (1868)
 "The Variations of Animals and Plants under Domestication"
 with a preface by Asa Gray
 Two Volumes
- Cole, Leon J. (1914)

 "Studies on Inheritance in Pigeons"

 1. Hereditary Relations of the Principal Colors.

 Bulletin 158. Agricultural Experiment Station of the Rhode Island State College. Kingston, R. I.,

 U. S. A. May 1914
- Cole, L. J. and Kelley, Frank J. (1919)

 "Studies on Inheritance in Pigeons III"

 "Description and Linkage Relations of two Sex-linked Characters"

 Reprinted from Genetics 4:183-203 March 1919
- Cole, L. J. and Kirkpatrick, William F. (1915)

 Sex Ratios in pigeons, together with observations on the laying, incubation and hatching of the eggs.

 Bulletin 162 Agricultural Experiment Station of the Rhode Island State College. Kingston, R. I., U. S. A. April 1915
- Crew, F. A. E. (1927)
 "The Genetics of Sexuality in Animals"
 MacMillan New York
- Fulton's Book of Pigeons, with standards for judging. Second edition edited by Rev. W. F. Lumley Canell and Company Ltd. London 1895
- Johansson, Ivar (1927)
 Studies on Inheritance in Pigeons VI
 "Number of Tail Feathers and Uropygial Gland"
 Reprinted from Genetics 12:93-107 March 1927
- Lloyd-Jones, 0. (1915)
 Studies on Inheritance in Pigeons II. A microscopical and chemical study of the feather pigments.
 Journal of Experimental Zoology 18 Vol. XVII pp. 453-509

BIBLIOGRAPHY (Continued) .

- Jones, Sarah Van Hoosen (1922)
 Studies on Inheritance in Pigeons IV
 Checks and Bars and other modifications of black
 Genetics VII, September 1922 pp. 466-507
- Metzelaar, Dr. Jan (1926)
 "Color Breeding in Pigeon Plumage"
 American Pigeon Keeper Geneva, Illinois 1926
- Metzelaar, Dr. Jan (1928)

 "Further Experiments in Inheritance of Color in Domestic Pigeons"

 No. 194 Published by University of Michigan, Museum of Zoology, Ann Arbor, Michigan April 4, 1928
- Riddle, 0. (1909)
 "Our Knowledge of Melanin Color Formation and its
 Bearing on the Mendelian Description of Heredity"
 Biological Bulletin 1909
- Riddle, 0. (1916)
 Sex-control and known correlation in Pigeons
 American Naturalist Volume 50 pp. 383-410
- Riddle, 0. (1917)

 The theory of sex as stated in terms of results of studies on pigeons.

 Science Volume 46 pp. 19-24
- Riddle, 0. (1924)
 A case of complete sex reversal in the adult pigeon.
 American Naturalist Volume 48 pp. 167-181
- Steele, Dewey G. (1925)

 "Studies of Inheritance in Pigeons V"

 "Lace or Silky, a Sex-linked Character"

 Journal of Heredity, Washington, D. C. Volume XVI

 No. 9 September 1925

The state of the s The same of family many to the same of the

